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Muscle attachment scars in a Carboniferous goniatite

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Abstract. A row of oval unpaired, ventral body attachment scars, accompanied by pseudosutures and drag bands, is preserved on surfaces of steinkerns of a lower Chesterian (Mississippian) goniatitid ammonoid, *Goniatites multiliratus*, from Oklahoma. Many smaller oval and crescentic attachment scars are present in the interspaces between these ventral attachment scars and between pseudosutures. Comparison with the muscle scars of other extant and fossil shelled cephalopods suggests that the unpaired ventral scars of this species represent the attachment sites of the muscle or ligament at the posterior end of the body. The smaller oval and crescentic scars on the ventral and lateral sides of each chamber appear to indicate weaker and less permanent attachments of muscular tissue to the shell wall. These are presumed to have been formed during gradual forward movement of the body.

Key words : Ammonoidea, Carboniferous, goniatites, mantle growth, muscle scar

Introduction

Various kinds of body attachment scars and impressions have been recognized on the inside shell surfaces and steinkerns of ammonoids (see Doguzhaeva and Mutvei, 1996, for a recent review). Two of the most common are : 1) suture-like impressions ("Pseudoloben" or pseudosutures) usually associated with spiral traces ("Schleppstreifen" or drag bands) (John, 1909 ; Bayer, 1977 ; Zaborski, 1986 ; Hewitt *et al*., 1991 ; Lominadze *et al*., 1993 ; Checa and Garcia-Ruiz, 1996) ; and 2) unpaired attachment scars on the mid-venter at the base of the body chamber (Crick, 1898 ; Jordan, 1968 ; Sarikadze *et al*., 1990 ; Weitschat and Bandel, 1991 ; Doguzhaeva and Mutvei, 1996). Pseudosutures and drag bands are currently interpreted as impressions made by the rear part of the mantle as it gradually moved forward (Hewitt *et al*., 1991 ; Checa and Garcia-Ruiz, 1996), while the mid-ventral attachment scar was probably the attachment site of the muscle or ligament that supported the circumsiphonal invagination at the posterior end of the body (Jordan, 1968 ; Doguzhaeva and Mutvei, 1996). These closely related types of scars and impressions are important in understanding the development of the growing mantle. However, they rarely co-occur in a single specimen, so previous studies of the growth of the ammonoid body in relation to new chamber formation have been based mainly on observations of pseudosutures and drag bands.

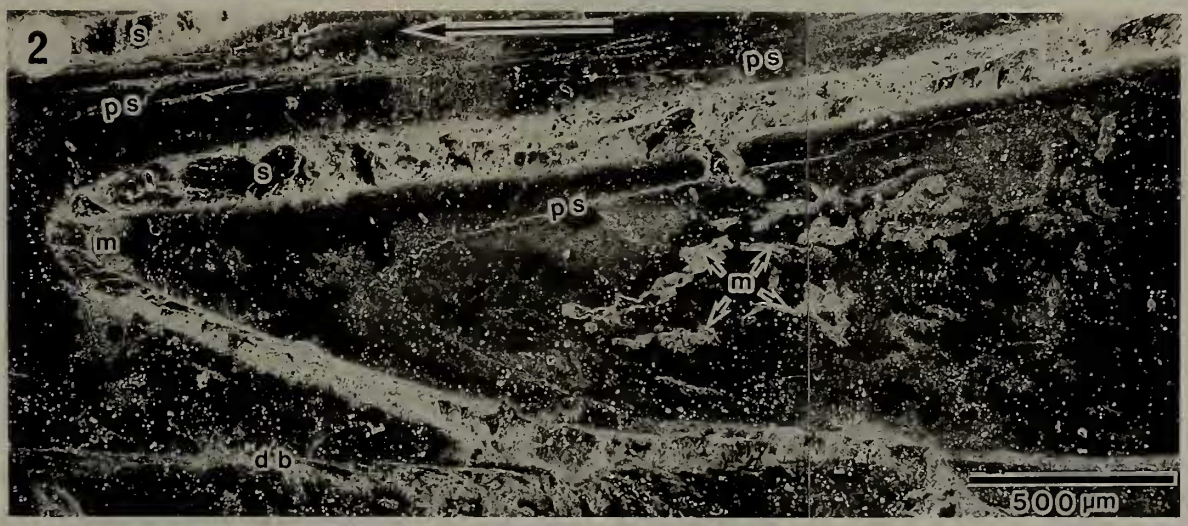
Here, two specimens of a Carboniferous goniatite in which both types of body attachment scars occur are described and their paleobiological implications are discussed.

Material and methods

Two immature specimens of *Goniatites multiliratus* Gordon (Goniatitina : Goniatitidae), both about 15 mm diameter, were examined. They were discovered in a calcareous concretion from the lower Chesterian (Mississippian) Caney Shale, exposed in Jack Fork Creek, Pontotoc County, Oklahoma (=Loc. M-1 of Mapes, 1979, fig. 2). We have previously

Figure 1. SEM micrographs showing muscle attachment scars and impressions on a specimen of the Mississippian ammonoid *Goniatites multiliratus* Gordon (UMUT. PM 19020-3). Arrows in 1 and 2 indicate the adoral direction. **1.** Unpaired ventral attachment scars (vm) on the adoral side of each mineralized septum (s). A pair of longitudinal drag bands (db) runs along the lateral margins of these scars. A sequence of pseudosutures (ps) and a cluster of small irregularly shaped attachment scars (m) are visible just adoral of the ventral lobe on the left side. **2.** Close-up of the adapical side of the first lateral saddle showing a cluster of small irregularly shaped attachment scars (m). **3.** Close-up of 2, showing a small irregularly shaped attachment scar adapical of the lateral saddle. **4.** Small attachment scar (m) just adapical of the first lateral saddle.


1
ps
db
vm
s
db
m
s
ps
ps
s
500 µm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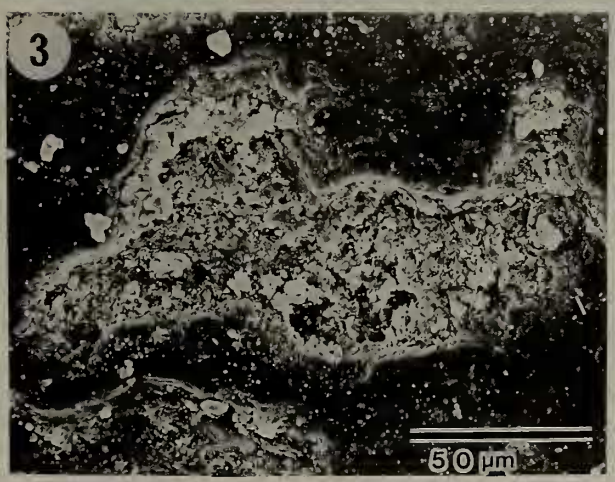
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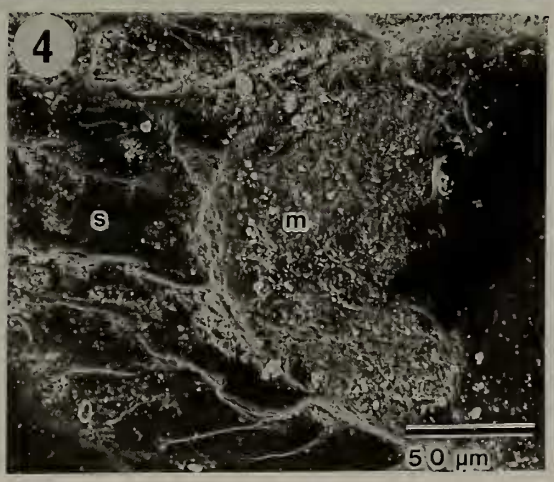
4
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1
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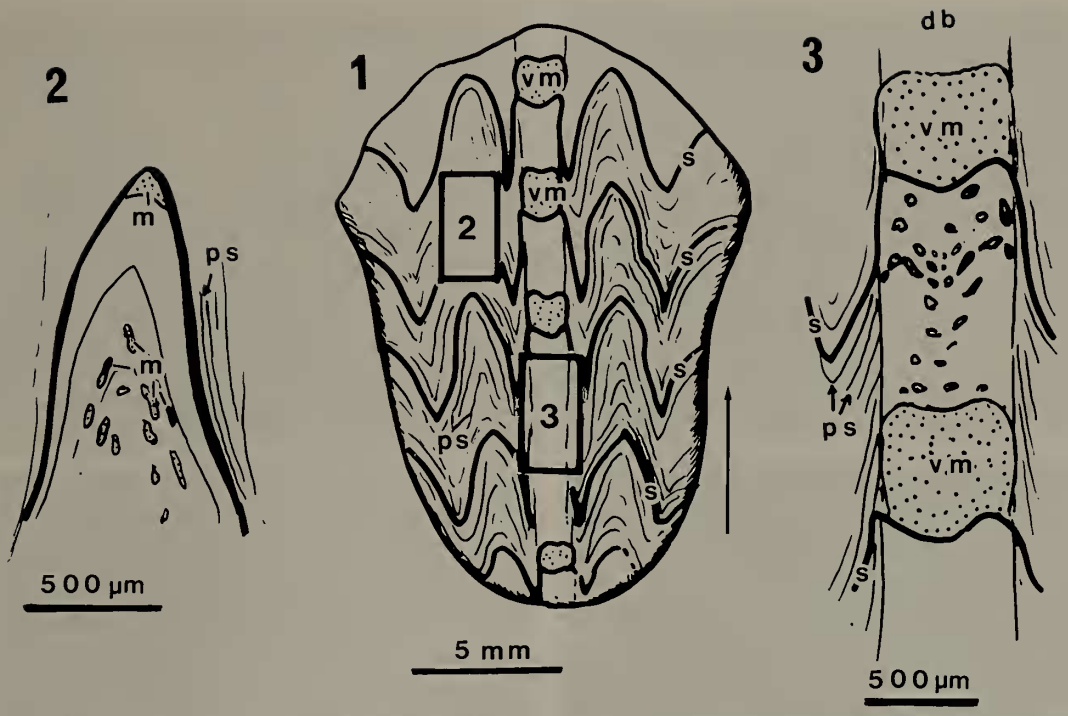

Figure 3. Diagrammatic drawing of a specimen of *Goniatites multiliratus* (UMUT. PM 19020-3), with unpaired ventral muscle attachment scars (vm) on the adoral side of each mineralized septum (s), that are accompanied by pseudosutures (ps) and darg bands (db). **1.** Frontal view. **2.** Close-up of the first lateral saddle portion, showing many smaller oval and crescentric attachment scars (m) in the interspaces between pseudosutures. **3.** Close-up of the mid-venter, showing the unpaired ventral muscle attachment scars (vm) and associated smaller attachment scars on the adoral side of each mineralized septum (s). The arrow indicate the adoral direction.

reported several specimens of the same species with pseudosutures and drag bands from this locality (Landman *et al.*, 1993). The two specimens were coated with platinum and then observed with a Hitachi Model S 2,400 scanning electron microscope.

For comparison, SEM observations were also made on the following extant and extinct cephalopods: 1) a specimen of *Spirula spirula* (Linnaeus) (Coleoidea: Spirulidae), with unpaired ventral attachment scars, which was caught alive in the waters off Surinam (810 m depth); 2) a specimen of the Callovian (Middle Jurassic) ammonite *Quenstedtoceras* sp. from Luków, Poland; 3) a specimen of the Desmoinesian (Pennsylvanian) orthocerid *Pseudorthoceras knoxense* (McChesney) from the Buckhorn Asphalt, Arbuckle Mountains, Oklahoma; and 4) a specimen of an indeterminate Late Mississippian member of the Aulacocerida from Durham, Arkansas. The specimens observed are housed in the American Museum of Natural History (AMNH) (aulacocerid specimen), Institut für Paläontologie, Universität Bonn (GPIBo) (orthocerid specimen), and the University Museum, University of Tokyo (UMUT) (remaining specimens).

Observations

In both specimens of *Goniatites multiliratus* examined, the body attachment scars, pseudosutures, and drag bands are preserved on the surfaces of the steinkerns. The attachment scars on the mid-venter are represented by a row of oval swellings on the adoral side of each ventral saddle (vm, Figures 1-1, 2-1, 3). In close-up, these scars are characterized by many small, round depressions with flat bottoms, each about 20-30 μm in diameter (Figure 2-2). This implies the presence of many small mounds on the surfaces of scars on the external shell (not preserved).

A pair of linear drag bands (db, Figures 1-1, 2-1, 3) runs longitudinally along the lateral margins of each scar. Rounded, oval, or more commonly irregularly shaped smaller attachment scars are visible in the interspace between paired drag bands, extending from the adoral side of one mid-ventral scar to the adapical side of the next (Figures 1-

Figure 2. **1.** SEM micrographs of unpaired ventral muscle attachment scars (vm) on a specimen of *Goniatites multiliratus* (UMUT. PM 19018-4); the lateral margins are marked by a pair of drag bands (db). The large oval scar just adoral of each mineralized septum (s) indicates a firm attachment of the muscle to the shell, while the cluster of smaller scars within each chamber suggests weaker and less permanent muscular attachment. The arrow indicates the adoral direction. db=drag band, s=septum, ps=pseudosuture. **2.** Close-up of the unpaired ventral muscle attachment scar, showing many small, round depressions with flat bottoms.

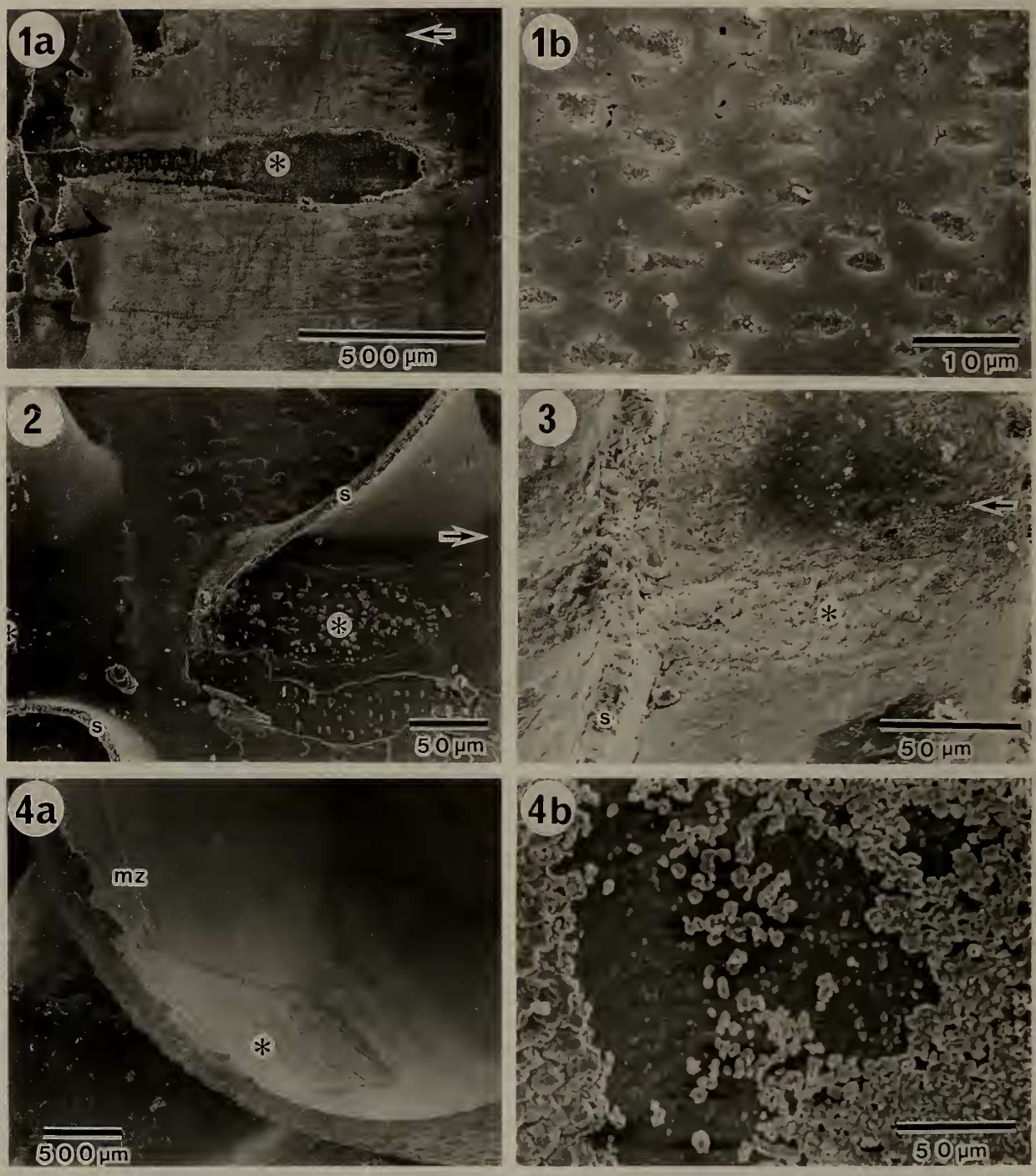

Figure 4. SEM micrographs of muscle attachment scars (asterisk) in selected shelled cephalopods. The arrows indicate the adoral direction. s : septum. **1a, b.** Unpaired ventral muscle scar and close-up on a steinkern of *Pseudorthoceras knoxense* (McChesney) (Orthocerida). GPIBo-Ri 90 from the Desmoinesian (Pennsylvanian) Buckhorn Asphalt, Arbuckle Mountains, Oklahoma (same specimen as that figured by Ristedt, 1971, pl. 34, fig. 2). **2.** Unpaired dorsal muscle scars on the inside shell surface of a specimen of *Quenstedtoceras* sp. (Ammonoidea : Ammonitina). UMUT. MM 19876 from the Callovian of Luków, Poland. **3.** Unpaired ventral muscle scar on the inside shell surface of a member of the Aulacocerida, gen. et sp. indet. (Coleoidea : Aulacocerida). AMNH 45338 from the middle Chesterian (Upper Mississippian), White River, Durham, Arkansas. **4a, b.** Unpaired ventral muscle scar on the inside shell surface of *Spirula spirula* (Linnaeus) (Coleoidea : Spirulidae). UMUT. RM 19874, Surinam (810 m depth).

1, 2-1, 3). A small attachment scar also occurs on the adapical side of the first lateral saddle in one of the two figured specimens (Figure 1-4). Many similar small oval and crescentic scars are present in the interspaces between pseudosutures (Figures 1-2, 1-3). All these attachment scars were originally expressed as shallow depressions or pores on the inside surface of the shell wall. There are no traces of organic remains (cameral membranes and/or gels) around the oval and crescentic scars.

Comparison and discussion

Preservation of muscle attachment scars is extremely rare in the Goniatitina and has only been documented in *Goniatites* and *Muensteroceras* (Crick, 1898 ; Jordan, 1968). The muscle scars of the two genera described by these authors differ from the unpaired ventral attachment scars of *Goniatites multiliratus* described herein and are both represented by dorsal paired attachment scars that occur on the anterolateral side of the steinkerns of the body chambers. In their shape and mid-ventral position within each chamber, the unpaired ventral attachment scars of *G. multiliratus* are comparable to those known from various Mesozoic ammonites (Crick, 1898 ; Jordan, 1968 ; Sarikadze *et al.*, 1990 ; see also Doguzhaeva and Mutvei, 1996, table 1 for a complete list of genera with this kind of attachment scar), members of the Orthocerida (Ristedt, 1971 ; Figure 4-1a, b) and Aulacocerida (Figure 4-3), and *Spirula* (Figure 4-4a, b). In extant *Nautilus*, the attachment site for the paired retractor muscles is located in the posterior region of the body chamber, where it is demarcated by the conspicuous ridge of the myoadhesive epithelial zone. Mutvei and Doguzhaeva (1997) demonstrated that the myoadhesive epithelium secretes a thick prismatic myostracal layer, consisting of bundles of vertically oriented acicular crystallites, at the attachment site to which the muscle is firmly attached. In *Spirula*, the myoadhesive epithelial zone is situated near the shell aperture (mz, Figure 4-4a). The myostracal layer at its muscle attachment site likewise consists of bundles of crystallites (Figure 4-4b). Bundles of crystallites are also observed on the unpaired ventral muscle scar in the aulacocerid specimen from Arkansas (Figure 4-3). Although the prismatic myostracal layer is not preserved in the two goniatite specimens examined here, the small, round depressions on the mid-ventral scars were presumably sites for attachment of bundles of crystallites secreted by the myoadhesive epithelium, as in *Nautilus*, *Spirula* and the Aulacocerida.

The unpaired mid-ventral muscle scars of *Goniatites multiliratus* (Figures 1, 2) are remarkably similar in their overall shape to unpaired dorsal attachment scars known from some Mesozoic Ceratitina (e.g. *Amphipopanoceras*, Lehmann, 1990, fig. 4.38) and Ammonitina (e.g. *Quenstedtoceras* and *Kosmoceras*, Bandel, 1982, pl. 13, figs. 3-5 ; *Euhoplites*, Landman and Bandel, 1985, fig. 31). In close-up, many small mounds of crystallites are developed on the inner surface of the dorsal scars in these genera (Figure 4-2).

Our observations strongly suggest that in *Goniatites multiliratus*, the unpaired ventral muscle was attached to the shell wall at the base of the body chamber for some time before formation of the next chamber. A similar condition is postulated for the unpaired dorsal muscle in some Mesozoic ammonites. In contrast, the round, oval, or irregularly shaped smaller pits observed on the ventral and lateral sides of each chamber (m, Figures 1-1, 1-2, 1-4) appear to indicate a weaker and less permanent attachment of muscular or ligamental tissue to the shell wall. These latter scars were presumably formed during the slow and stepwise forward movement of the body during growth.

As our data indicate, there are still many questions regarding the attachment of the soft body to the shell. A variety of models have been proposed to explain septal morphogenesis and the forward movement of the body (e.g., Checa and Garcia-Ruiz, 1996), but most of them lack comparative anatomical background. Are all the pseudosutures we observed related to pseudosepta and/or to the presence of so-called cameral gel ? Are the small oval and crescentic scars between pseudosutures present in other ammonoids ? How do all these different kinds of attachment scars fit in with the tie point model of septal formation (e.g. Seilacher, 1988) and with the more recent model of the "Cartesian Diver" (Seilacher and LaBarbera, 1995)? Future studies of well-preserved material and comparison with the anatomy of extant cephalopods may yield solutions to these problems.

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